

ANALYSIS OF A PROGENY TEST OF A HYBRID OAK,  
*QUERCUS GAMBELII* × *Q. TURBINELLA*

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Natural hybrids between *Quercus gambelii* Nutt. and *Q. turbinella* Greene (figs. 1–3) are known from numerous locations in Utah and Arizona (Cottam, Tucker, and Drobnick, 1959; Tucker, Cottam, and Drobnick, 1961). They commonly occur in northern Arizona and southern Utah, where the parental species are sympatric, but many have also been found farther north in Utah beyond the northern limits of *Q. turbinella*. Indeed, the most northerly hybrid location is some 260 miles beyond the present northern limits of *Q. turbinella*. This anomalous situation seems to be best explained by the hypothesis that the range of *Q. turbinella* extended farther north at some time in the past, the most likely time being the post-Pleistocene Altithermal period. This period, which extended from about 7500 to 4000 years ago, was marked by a warmer climate than at present; this would have provided the necessary environmental conditions for the northward migration of *Q. turbinella*. As the climate subsequently became cooler, *Q. turbinella* was eliminated in these northern areas but not before it had produced numerous hybrids with the common, widespread *Q. gambelii*. Many of these hybrids have persisted to the present time (see Cottam et al., 1959).

In a detailed analysis of these field hybrids (Tucker et al., 1961), morphological intermediacy was taken as proof of their hybridity. It was acknowledged that direct genetic evidence would also be desirable, and it was mentioned that progeny tests were in progress (Tucker et al., 1961, p. 332). Another procedure, of course, would have been experimental synthesis of the hybrid by crossing the two presumed parents. Both procedures have now been successfully pursued. Cottam and Drobnick have experimentally crossed *Q. gambelii* and *Q. turbinella* several times (unpubl. data), with the resulting hybrids differing in no significant morphological detail from the natural hybrids. Our paper reports the results of a progeny test performed with a large collection of acorns from a single natural hybrid in Utah.

The parent hybrid is a large shrub growing in Coon Canyon in the Oquirrh Mountains, Salt Lake County, Utah. It was discovered by Rudy Drobnick in the course of a M.S. study at the University of Utah. Here, at an elevation of 5300 feet, on a south exposure, it was surrounded by shrubs of *Q. gambelii*. In 1957 it bore a heavy crop of acorns, and on September 10, 1957, a large collection (*Drobnick 10*,



FIG. 1-3. 1, Representative specimen of *Quercus gambelii* (Tucker 2826-9); 2, specimen from the hybrid, *Q. gambelii* × *Q. turbinella*, Oquirrh Mountains, Salt Lake County, Utah (Drobnick 10-1); 3, representative specimen of *Q. turbinella* (Tucker 2810-1).

which included a voucher specimen, now on file at U.C., Davis, fig. 2) was made and sent to the senior author. The acorns were quite variable in size, and it was thought that the smaller ones might have less fully developed embryos than the larger ones; but there was also a possibility that the smaller ones might represent individuals closer to *Q. turbinella* (for the latter species has smaller acorns and smaller embryos than *Q. gambelii*). Therefore, rather than run the risk of biasing our results by rejecting them, the small acorns were sown in roughly the same proportion as their occurrence in the sample as a whole.

As a secondary experiment, groups of 100 of the larger acorns and 100 of the smaller ones were sown under comparable conditions. A somewhat higher percentage of the larger germinated, 83 compared to 68 of the smaller ones. Although this was inconclusive evidence, it tended to strengthen our suspicion that the smaller acorns might be "weaklings", containing less fully developed embryos.

Altogether, 900 acorns were sown. A total of 708 seedlings was obtained, but by March 24, 1958, the number had diminished to 522. These were planted out in a plot in the University Arboretum during the spring of that year. The project was terminated after seven growing seasons, and on August 26 and 27, 1964, the individual heights of the 183 survivors were measured and a voucher specimen collected from each.

Over the period of this progeny test, conspicuous variation in size and general vigor had become apparent. At the termination of the project, the hybrids ranged from moribund dwarfs a few centimeters in height to vigorous, freely branching individuals well over two meters tall. In gross morphology, also (notably size, form, and color of the leaves), the hybrids were extremely variable. Those with the smallest leaves closely approached the maternal parent. It was interesting that none was noticeably more *turbinella*-like than the parental hybrid, i.e., none had leaves that were noticeably paler in color, less deeply lobed, or more spinose. Instead, the great majority were more suggestive of *Q. gambelii*, and several individuals would have been readily identified as this species (fig. 4). Indeed, the whole aspect of the group indicated a backcross generation to *Q. gambelii*.

Although there was a high rate of attrition in the progeny (522 planted out in 1958; only 183 survivors in 1964), it seems quite unlikely that the absence of any *turbinella*-like individuals was due to a higher mortality rate among them than among the *gambelii*-like individuals. Indeed, if there had been differential survival (and there may have been), any *turbinella*-like individuals should have been better adapted to the hot, dry summers of the Sacramento Valley than the more *gambelii*-like individuals.

*Analysis of the progeny.* Individuals in the progeny were analyzed (by Bogert) using the same procedures as in the study of the natural

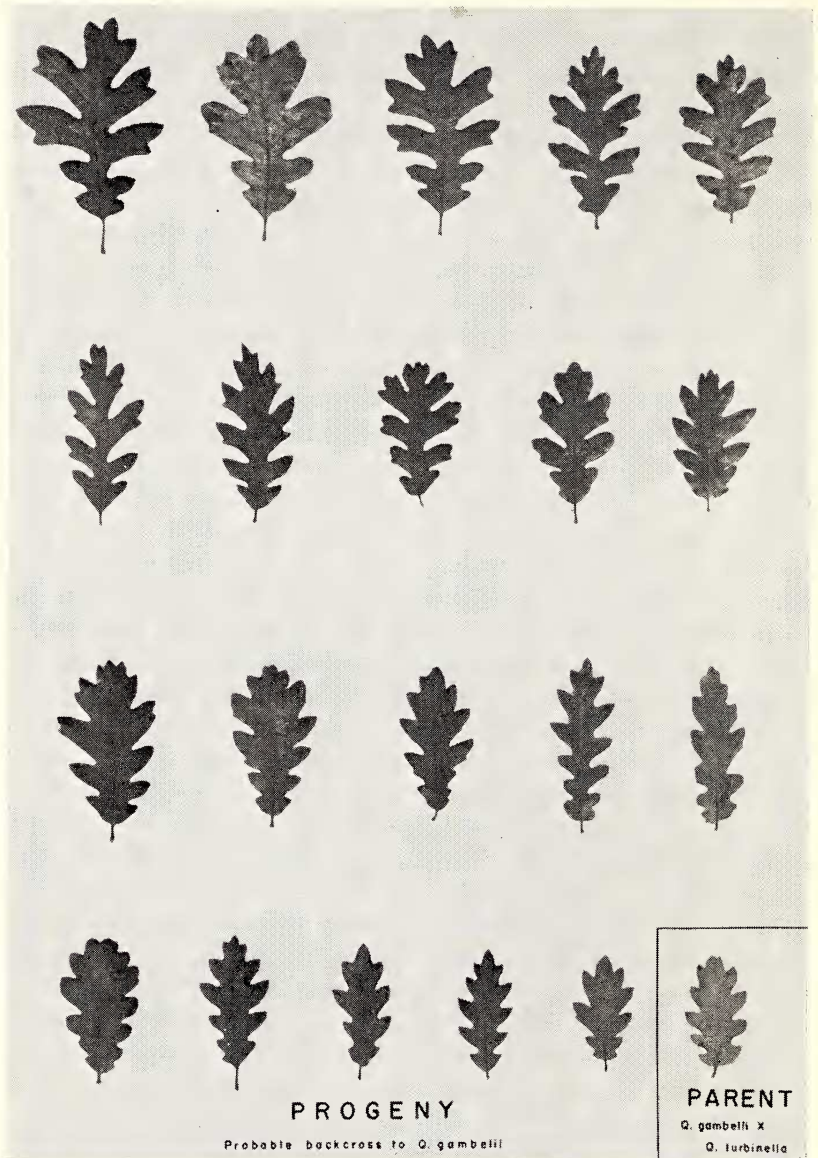


FIG. 4. Leaves from selected individuals in the hybrid progeny (a single representative leaf taken from each). This small sample of the progeny shows the range of leaf forms, from the largest and most *gambelii*-like, to the smallest, and most like the maternal parent. The greater part of the progeny, however, had leaves more similar to one form or another in the two middle rows.

hybrids (Tucker et al., 1961). The characters analyzed were: (1) leaf length, (2) relative depth of lobing (vein:lobe ratio), (3) mean number of rays per stellate hair, (4) leaf color, (5) apex of marginal teeth or lobes, and (6) density of twig pubescence. The data from our analysis are presented as a frequency histogram (fig. 5) using Anderson's (1936) hybrid index method. Every specimen was scored on each of the six characters stated above. The condition typical of *Q. turbinella* was given a score of zero, that of *Q. gambelii* a score of two, and an intermediate condition of a score of one. The quantitative characters (No. 1, 2, and 3, of the six mentioned above) were scored according to the following scheme:

Character	<i>Q. turbinella</i> (score: 0)	Intermediate (score: 1)	<i>Q. gambelii</i> (score: 2)
leaf length	36 mm or less	37-63 mm	64 mm or more
vein:lobe ratio	2.41 or more	1.75-2.40	1.74 or less
mean ray no. per stellate hair	8.0 or more	4.1-7.9	4.0 or less

The qualitative characters (No. 4, 5, and 6) were judged using the same "standard specimens" (with one exception) that were used in the study by Tucker et al. (1961). The total score possible would thus range from zero (for an individual scored as *turbinella* on all six characters) to twelve (for an individual scored as *gambelii* on all six).

The resulting index totals for the hybrid progeny are presented in Figure 5. Presented for comparison are similar index totals for population samples of *Q. turbinella* and *Q. gambelii*. These are the same collections from which the data were included as pictorialized scatter diagrams in the study by Tucker et al. (1961, fig. 3, 4).

It is evident that the points regarding the nature of the progeny deduced from inspection of gross morphology, mentioned previously, are borne out by our analysis. The great majority of the progeny tends to be more *gambelii*-like than the maternal parent (the original hybrid in the Oquirrh mountains), and only four in the entire progeny had index totals as low as its total (7). Assuming that the mean hybrid index value of a backcross progeny would be midway between that of the F<sub>1</sub> (7) and the score for pure *Q. gambelii* (12), we would thus expect a value of 9.5. The actual mean of the progeny was 9.7, a value very close to expectation.

A breakdown of the number of individuals scored on each character as *gambelii*, as intermediate, and as *turbinella*, is given in Table 1. It is apparent that only one individual, on a single character (leaf length), was scored as *turbinella*.

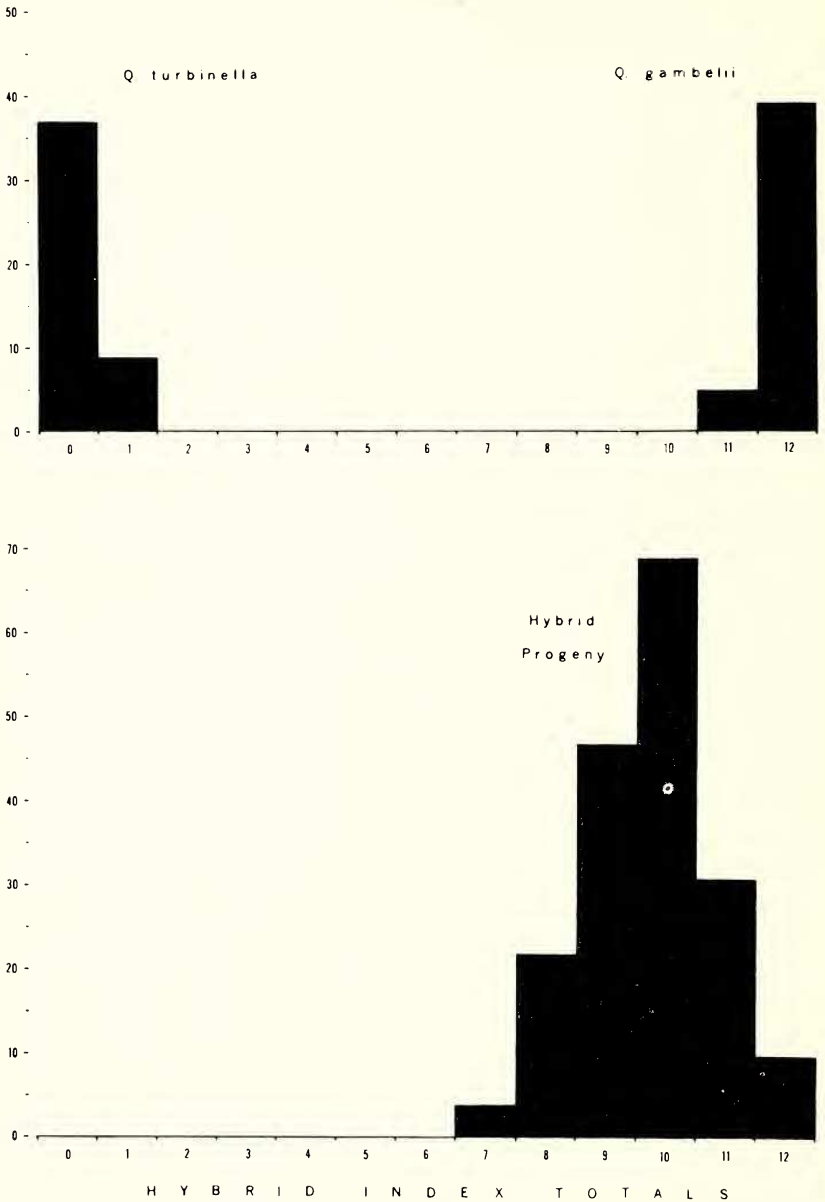


FIG. 5. Frequency histograms of hybrid index totals for (above) two combined population samples of *Q. turbinella* (Tucker 2810 and 2813) (left), and two combined population samples of *Q. gambelii* (Tucker 2775 and 2826) (right); and (below) the hybrid progeny. (Vertical scale at left indicates number of individuals.)

TABLE 1. CHARACTER ANALYSIS OF HYBRID PROGENY

Character	Scored as <i>gambelii</i>		Scored as intermediate		Scored as <i>turbinella</i>	
	No.	%	No.	%	No.	%
leaf length	(64 mm or more)		(37-63 mm)		(36 mm or less)	
	36	19.7	146	79.8	1	0.5
vein: lobe ratio	(1.74 or less)		(1.75-2.40)		(2.41 or more)	
	169	92.3	14	7.7	0	0
leaf color	84	45.9	99	54.1	0	0
lobe apex	144	78.7	39	21.3	0	0
twig pubescence	78	42.6	105	57.4	0	0
rays per stellate hair	(4.0 or less)		(4.1-7.9)		(8.0 or more)	
	170	92.9	13	7.1	0	0
Totals:	681	62.0	416	37.9	1	.1

*Discussion and conclusions.* There can be little doubt that the parent shrub in the Oquirrh Mountains was a hybrid. This is indicated not only by its morphological intermediacy, but also by the highly variable nature of the progeny, which at one extreme includes individuals very similar to the mother plant and at the other extreme a few individuals indistinguishable from *Q. gambelii*.

In a discussion of oak hybrids, Stebbins (1950, pp. 64-65) expressed the following views: "One interesting feature of the progeny of both artificial and natural oak hybrids is that in respect to vegetative characteristics they usually segregate so sharply that even among a relatively small number of individuals the parental types can be recovered (MacDougal 1907, Ness 1927, Coker and Totten 1934, Allard 1942, Wolf 1938, 1944, Yarnell 1933, and Stebbins, unpublished). This is in striking contrast to the behavior of interracial and interspecific hybrids in most other plant groups, in which the number of genetic factors controlling the differences between them is so large that it is relatively difficult to recover the parental types . . . . The evidence available suggests that the number of genes by which species of oaks differ from each other is considerably smaller than it is in the case of most other plant groups."

There are several points in the foregoing statement on which we would like to comment. First, the statement that vegetative characteristics usually segregate sharply is quite contrary to our experience. The senior author has yet to see a sizeable oak progeny that did not show a *graduated series* of forms from one extreme to the other. Indeed, of the oak studies cited by Stebbins, the only one that purports to show sharp character segregation was that of Yarnell (1933), but in our opinion, Yarnell's interpretation of his results is open to question. He analyzed

a single character (leaf size) in 20 second generation trees from seven  $F_1$ 's (that Ness, 1918, had originally produced by experimentally crossing *Quercus virginiana* and *Q. lyrata*). Yarnell's values show essentially a bimodal distribution. He referred to these second generation trees as " $F_2$ 's", but when his study is carefully analyzed it seems much more likely that they were a composite of two backcross generations—one to each of the parental species, both of which were planted in the area (see Yarnell, 1933; also, Ness, 1918; 1927, p. 385). On this basis, a bimodal distribution would have been expected.

In the other oak studies cited by Stebbins, although the hybrid progenies were commonly referred to as " $F_2$ 's", in most instances it is more likely that they were backcrosses. In all cases they were grown from acorns resulting from open pollination, with the source of the pollen unknown. Oak hybrids commonly occur as isolated  $F_1$  trees growing with the parental species, and the progeny of an  $F_1$  (when it is fertile) will usually result from backcrossing to one parent or the other, rather than from self-pollination (Palmer, 1948). Self-pollination experiments with oaks have usually indicated a moderate to high degree of self-incompatibility (Pjatnitskii, 1934; Wright, 1953; Schreiner, unpubl.).

In regard to the recovery of parental types in hybrid progenies, Anderson has pointed out (1949, pp. 25–26) that parental types may be expected to occur with higher frequency in a backcross generation than in an  $F_2$ . As most authors have used the term, a "parental type" seems to be an individual resembling one parent quite closely, but that, one suspects, might show slight suggestions of the other parent when scrutinized very closely. In the oak studies cited by Stebbins, "parental types" were judged solely on leaf characters and did not include acorn, twig, or bud characters. Thus, such "parental types" were judged on the basis of very incomplete analyses, perhaps more so than in similar studies in other plant groups.

In any event, "parental types", as close approximations of the phenotype of the recurrent parent, do not seem to be particularly rare in first backcross progenies, as evidenced by studies in *Carthamus* (P. F. Knowles, pers. commun.), *Downingia* (Wood, 1961), *Geum* (Marsden-Jones, 1930), *Helianthus* (Long, 1966), *Phacelia* (Gillett, 1955), *Solidago* (Goodwin, 1937), and *Vernonia* (Jones, 1966). Therefore, the genus *Quercus* may not be as different from other plant groups as has been supposed.

Finally, to summarize briefly the results of this study, a progeny test was made with acorns from a natural hybrid of *Q. gambelii*  $\times$  *Q. turbinella* in the Oquirrh Mountains in Utah. The hybrid was growing with *Q. gambelii*, but not with *Q. turbinella*, which does not occur in that region. Seedlings of the progeny were analyzed on six morphological characters, which distinguish the parental species. The progeny showed great variation in all these characters, as well as in size and vigor. This



extreme variation in the progeny is corroborative evidence of the hybrid nature of the maternal parent; and the results of the analysis indicate that the progeny was probably a backcross to *Q. gambelii*.

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